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Offspring beg more towards larger females in a burying beetle

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Lay summary

We find that burying beetle larvae beg more toward larger females when given a choice between two females: a larger and a smaller one. Our results suggest that, for animals that breed in groups, offspring may beg more towards the larger caregiver, which is likely to provision offspring with more food. Furthermore, they show that offspring can choose between caregivers based on difference in body size between them and adjust their begging behaviour accordingly.

Abstract

Offspring of many animals beg for food from parents. Begging is often costly, and offspring should seek to reduce such costs to maximise their returns on begging. Whenever multiple adults provide care for a joint brood, as in species where multiple females breed communally, offspring should beg towards the parent that provisions the most food. Here, we investigate whether larvae spend more time begging towards larger females in the burying beetle *Nicrophorus vespilloides*. Prior work on this species shows that larger females provision more food than smaller ones, suggesting that larvae would benefit by preferentially begging towards larger females. To test for such a preference, we provided experimental broods with a simultaneous choice between two dead females: a smaller and a larger one. Larvae spent more time begging towards larger females. We next examined the behavioural mechanism for why larvae begged towards larger females. Larvae spent more time in close contact with larger females over smaller ones, whilst there was no evidence that larvae begged more *when* in close contact with larger females. Thus, larvae begged more towards the larger female simply as a consequence of spending more time close to larger females. Our findings have important implications for our understanding of parent-offspring communication by showing that offspring can choose between parents based on parental attributes, such as body size, reflecting how much food parents are likely to provision.

Keywords: begging, body size, *Nicrophorus vespilloides*, parent-offspring communication, parental care.

Introduction

Offspring beg for food from their parents across many animal taxa, including birds (e.g. Budden and Wright, 2001), mammals (e.g. Smiseth and Lorentsen, 2001), amphibians (e.g. Yoshioka et al. 2016) and insects (e.g. Rauter and Moore, 1999). Theoretical models propose that costly offspring begging behaviours evolved as a behavioural mechanism for resolving parent-offspring conflict over parental care (Godfray 1991; Parker et al. 2002). The reason for this is that costs of begging ensure that parents benefit by adjusting their food provisioning in response to begging because parents obtain honest information on the nutritional need of their offspring. There is empirical evidence that begging often incurs costs to offspring in terms of reduced growth (e.g. Kilner 2001; Takata et al. 2019), increased risk of predation (e.g., Haskell 1994; Redondo and Castro 1992), or increased mortality due to filial infanticide (e.g., Andrews and Smiseth 2013). When begging is costly, offspring should be under selection to maximise their returns on begging (Bell 2008; Madden et al. 2009). For instance, in species where both parents provision food for the offspring, and where parents of one sex provision more food than the other, offspring may maximise their returns on begging by begging more towards parents of the sex that provisions the most food, as reported in studies on birds (e.g. Kölliker et al. 1998; Roulin and Bersier 2007; Dickens et al. 2008) and insects (Suzuki 2015; Paquet et al. 2018).

Although there is good evidence that offspring beg more towards parents of the sex that provisions the most food, it is unclear whether begging offspring also respond to other attributes of their parents that might predict the offspring's returns on begging, such as the body size, nutritional state, or age of parents. For example, offspring may beg more towards larger parents if they provision more food than smaller ones. Larger parents produce more milk than smaller parents in mammals (Landete-Castillejos et al. 2003), provision food more often to the nest in insects (Bosch and Vicens 2006), and provision larger loads of food in

birds (Tveera et al. 1998). Whenever multiple adults provide care for a joint brood, offspring could potentially maximise their returns on begging by begging more towards the larger adult. Species with communal breeding, where multiple females breed on a shared resource or in a joint nest (Vehrencamp 1978, 2000; Koenig and Dickinson 2004), are particularly useful to test whether offspring beg more towards larger adults given that caring adults differ with respect to body size only. In contrast, caring adults also differ with respect to sex and breeding status (i.e., parent versus helpers) in the contexts of biparental care and cooperative breeding, respectively, in which case there may be confounding effects due to the sex and breeding status of adults.

Here, we conducted an experiment on the burying beetle *Nicrophorus vespilloides* in which we tested whether larvae begged more towards larger females than towards smaller ones. Burying beetles of the genus *Nicrophorus* are ideal study species to explore this issue because multiple females sometimes breed communally on a shared resource: the carcass of a small vertebrate (Eggert and Müller 1992; Trumbo 1992). Communally breeding females provide care indiscriminately to any larva in the joint brood (Komdeur et al. 2013; Richardson and Smiseth 2020). Communally breeding females may differ in body size when breeding on large carcasses (Eggert & Müller, 2000), suggesting that larvae sometimes are in a position to choose between different-sized females. Larger females spend more time provisioning food to the brood than smaller females (Steiger 2013) and may process food more efficiently than smaller ones (Pilakouta et al. 2015). Thus, given that begging incurs costs to larvae in terms of increased mortality and reduced growth (Andrews and Smiseth 2013; Takata et al. 2019), larvae might maximise their returns on begging by begging more towards larger females.

Our first aim was to test the hypothesis that larvae maximise their returns on begging by begging more towards larger females. We used a simultaneous choice design, in which larvae could choose between one larger and one smaller female. The hypothesis predicts that

larvae would beg more towards the larger female. Our second aim was to test two potential behavioural mechanisms for why larvae begged more towards the larger female. First, larvae may respond directly to female body size by begging more when they are in close contact with the larger female. Second, larvae may respond indirectly by spending more time in close contact with the larger female, thereby having more opportunities to beg towards the larger female. The first mechanism predicts that larvae would beg more when they were in close contact with the larger female as opposed to when they were in close contact with the smaller one, but that there would be no difference in the amount of time that larvae spend in close contact with the larger or the smaller females. The second mechanism predicts that larvae would spend more time in close contact with the larger female than with the smaller female, but that larva would not beg more when they were in close contact the larger. These two mechanisms are not mutually exclusive, and it is therefore possible that larvae would beg more when they were in close contact with the larger female and spend more time in close contact with the larger female.

Materials and methods

Origin and rearing of experimental beetles

The beetles used in the experiments descended from individuals collected in the wild in the Hermitage of Braid and Blackford Hill Local Nature Reserves, Edinburgh, UK. The beetles had been kept under laboratory conditions for at least three generations. We kept the stock population outbred by breeding a large number of individuals each generation, recruiting only three individuals from each family to the next generation, outcrossing our stock population with wild-caught beetles each summer, and avoiding breeding between close relatives (see Matthey et al. 2018). We maintained our laboratory population at constant temperature (20 °C) and under a 16:8h light:dark photoperiod. Non-breeding adult beetles were housed in

individual transparent plastic containers (12 cm × 8 cm × 2 cm) filled with moist soil, and were fed small pieces of organic beef twice a week.

Experimental design

We used a simultaneous choice design, in which larvae could choose between two dead females – one larger and one smaller (Paquet et al. 2018) – because such designs are better at detecting preferences than alternative sequential choice designs (Dougherty and Shuker 2014). This design is biologically realistic for our species given that females will breed communally on large carcasses (Eggert and Müller 1992; Komdeur et al. 2013; Richardson and Smiseth 2020). We used dead females as stimuli to exclude any potential effects of differences in the behaviour of larger and smaller females that might affect larval behaviour. Prior work shows that larvae beg towards dead parents in a similar way as they do towards live ones (Smiseth and Parker, 2008; Mäenpää et al. 2015; Paquet et al. 2018).

Experimental procedures

At the start of the experiment, we generated the smaller and larger females that we later used as stimuli when investigating larval begging towards larger and smaller females. We generated these females following established protocols (Steiger 2013; Pilakouta et al. 2015). To this end, we matched 34 pairs of unrelated males and females from our stock population by providing them with a mouse carcass to initiate breeding. To manipulate female body size, we removed larvae from each of these 34 the carcasses at two different stages in their development: when they had reached a mass of 100–150 mg (mean mass ± SE at dispersal: 0.130 g ± 0.004) and when they had reached a mass of 200–250 mg (mean ± SE mass at dispersal: 0.222 g ± 0.003). The former larvae were destined to become smaller adults, whilst the latter were destined to become larger adults. From each brood, we aimed to remove a

similar number of larvae that had reached a mass of 100–150 mg and that had reached a mass 200–250 mg. Given that larval mass at the time of dispersal from the carcass determines adult body size (Lock et al. 2004), these treatments allowed to generate a difference in size between females. The treatment was effective as larger females had a pronotum width (mean \pm SE: 5.08 ± 0.03 mm) that was on average 23% larger than that of the smaller females (mean \pm SE: 4.10 ± 0.02 mm).

Once removed from the carcass, larvae destined to become smaller or larger adults were placed in individual containers (12 cm \times 8 cm \times 2 cm) filled with moist soil until they eclosed as adults. After eclosion, we sexed all adults, keeping females only for use in our experiment. We kept all smaller and larger females in individual containers for a minimum of 10 days after eclosion to allow them sufficient time to undergo sexual maturation. During this period, we fed all females small pieces of organic beef twice a week until they were used in our experiment. Insect species that undergo complete metamorphosis cease growing once they reach adulthood. Thus, feeding adult females will have no effect on their body size, although it will have an impact on their adult body mass.

Once the females reached sexual maturity, we randomly selected 32 larger and 32 smaller females for use in our experiments. These females were first used to produce larvae for the experimental broods, and later as foster parents and stimuli during our behavioural observations (see below). To initiate breeding, we paired each female with an unrelated male from our stock population, placed each pair in a larger container (17 cm \times 12 cm \times 6 cm) with 2 cm of moist soil, and provided them with a defrosted mouse carcass of a standardized size (20.01–23.64 g) (Livefoods Direct, Sheffield). We checked the containers daily for the presence of eggs, defining the onset of egg-laying as the day on which the first eggs were laid. Two days after the outset of egg-laying (corresponding to the day preceding the expected time of hatching; Smiseth et al. 2006), we separated each female from her eggs by transferring

females and their carcasses into fresh containers lined with moist soil. We did this to ensure that no other larvae were present when we later allocated females with a donor brood (see below). Females lay their eggs asynchronously (Smiseth et al. 2006). We therefore separated females from the eggs two days after the start of eggs because this coincides with a time in the breeding cycle where females had ceased egg laying but where the first egg had yet to hatch. At this time, we removed the male to exclude any potential effects of male presence on larval begging. There is no evidence that the removal of the male has any detrimental effects on offspring growth or survival under laboratory conditions (Smiseth et al. 2005).

We generated 32 donor broods by pooling newly hatched larvae from across multiple broods. All such broods were comprised of 10 same-aged larvae of mixed maternity. Once assembled, donor broods were allocated at random to a smaller or a larger female foster parent. Females have a temporal kin discrimination mechanism, culling any larvae that hatch earlier than the expected time of hatching of their own eggs (Müller and Eggert 1990). We therefore provided females with a donor brood only after her own eggs had started hatching. Given that donor broods were composed of larvae of mixed maternity, most larvae would be genetically unrelated to their foster female. We used donor brood to generate experimental broods of 10 larvae immediately before the start of our behavioural observations (see below). We used experimental broods to exclude any potential confounding effects due to natural variation in brood size (Ratz and Smiseth 2018), larval age (Smiseth et al. 2007a; Smiseth et al. 2007b), or age composition within the brood (Smiseth and Moore 2007) on larval behaviour.

Larval begging

We conducted the behavioural observations 24 h (\pm 15 min) after we had allocated an experimental donor brood to a foster female when larvae had reached their second instar

(Smiseth and Moore 2002). We did our observations at this stage in larval development because it coincides with a peak in time spent begging for food from their parents (Smiseth et al. 2007a; 2003). Approximately 1 h before the start of each behavioural observation session, we sacrificed the females to be used as stimuli to trigger larval begging by freezing them at -20°C for 30 min. These females had previously produced larvae for our experimental broods and had therefore been caring for larvae during the 24 h preceding the observation. We used breeding females as stimuli because larvae beg more towards breeding females than towards non-breeding ones (Smiseth et al. 2010). We then thawed the females at ambient temperature for a minimum of 10 min to ensure that we could position their body and legs (see below).

We generated experimental broods comprised of 10 larvae from the donor broods. We always assigned experimental broods to a pair of unfamiliar dead females to exclude any potential confounding effects should larvae behave differently towards familiar and unfamiliar females (Mäenpää et al. 2015). All experimental broods were comprised of 5 larvae that had been reared by a larger female and 5 that had been reared by a smaller female. This procedure ensured that all experimental broods comprised an equal number of larvae that had prior exposure to a larger and a smaller female. Thus, if larvae learned a preference for larger or smaller females depending on their prior exposure to a larger and a smaller female, this would be detected as 5 larvae being in close contact with each of the two females. We confirm that this was not the case as, on average, eight larvae were in close contact with one female and one with the other. We placed the 10 larvae in a small container (11 cm \times 11 cm \times 3 cm) lined with moist paper towel 30 min prior observation to ensure that the larvae were not fully satiated and therefore motivated to beg at the start of the observation. Just before the start of the observation sessions, we pinned the larger and smaller females near the centre of the box (Figure 1a), and positioned them such that they mimicked a parent provisioning food

(Mäenpää et al. 2015; Paquet et al. 2018; Figure 1b). We then placed all larvae in front of the two females such that they were equidistant from them (Figure 1a). We allowed a 5-min acclimation period before we started the observation session.

We observed larval behaviour using instantaneous recording, noting the number of larvae that were begging towards each female and the number of larvae that were in close contact with each female every 60 s for 15 min. We defined larval begging as when larvae touched any body part of a female with their legs (Smiseth et al. 2003; Figure 1b). We defined larvae as being in close contact with a female as the larvae being closer to the female than the width of her pronotum (Rauter and Moore 1999). We first calculated the mean proportion of time spent begging per larva in the brood towards each female (B) as the number of begging events towards each female across the 15 scans (Σb) divided by the number of sampling scans (15) and the number of larvae in the brood (10), as $B = (\Sigma b/15)/10$. This metric used information of larval begging only and represents the overall mean time spent begging per larva in the brood towards each female.

Behavioral mechanisms

We next investigated two potential behavioural mechanisms for why larvae might beg more towards the larger female. First, larvae may respond directly to female body size by begging more when they were in close contact with the larger female. We calculated the mean proportion of time spent begging per larva when larvae were in close contact with either the larger or the smaller female (B') as the number of begging events towards each female across the 15 scans (Σb) divided by the total number of counts of larvae being in close contact with the female in question across the 15 scans (n), as $B = \Sigma b/n$. This metric differs from one above because it takes into account potential differences in the amount of time that larvae spent in close contact with each female.

Second, larvae may respond indirectly to female body size by spending more time in close contact with the larger female, thereby having more opportunities to beg towards her. We recorded the total number of counts of larvae being in close contact with the female in question across the 15 scans. Given that the number of larvae that were close to the larger female is inversely related to the number of larvae that were close to the smaller one, we focused on the proportion of larvae in the brood that associated with the larger female. We calculated the proportion of larvae that were in close contact with the larger female (C) as the number of counts of larvae being close to the larger female across the 15 scans (Σc) divided by the number counts of larvae being close to either one of the two females across the 15 scans (n), as $C = \Sigma c / n$.

Statistical analysis

All statistical analyses were conducted using R version 3.6.0 (R Development Core Team 2019) loaded with the packages *car* (Fox et al. 2016), *MASS* (Ripley et al. 2017), and *lme4* (Bates et al. 2014). We first investigated whether larvae begged more towards the larger female. To do so, we tested whether there was a difference in mean proportion of time spent begging per larva towards larger and smaller females. Given that these data represented the proportion of time that larvae spent begging, we used generalized linear mixed models with a binomial distribution. We included female body size (larger or smaller) as a fixed effect and brood ID and observation level as random effects to account for repeated measures on the same broods and to handle overdispersion (Harrison 2005). We then tested whether larvae begged more when were in close contact with the larger female using a generalized linear mixed model with a binomial distribution. We included female body size (larger or smaller) as a fixed effect and brood ID and observation level as random effects. Finally, we tested whether larvae spent more time in close contact with the larger female. To this end, we used a

Wilcoxon signed-rank test comparing the observed proportion of larvae that were in close contact with the larger female against the null expectation of 0.5 as expected if larvae spent an equal amount of time in close contact with the two females (Crawley 2005).

We excluded 10 broods out of 32 broods from our analyses because at least one of the two females later used as stimuli during our experiments had not been observed at the carcass at the time we removed the females from their original container. We excluded these females because such females had deserted their brood. We did this because prior work shows that breeding and non-breeding females have different cuticular chemical profiles (Müller et al. 2003; Steiger et al. 2007), and that larvae have a strong preference for begging towards breeding females over non-breeding ones (Smiseth et al. 2010). Thus, we excluded cases where one of the females had deserted the brood prior to the observation to exclude potential confounding effects due to another factor that is likely to influence larvae begging behaviour (i.e., female breeding status). The final sample size in our study was thus 22 broods.

Results

We first tested for a difference in the overall time spent begging towards the larger and smaller females. Larvae spent on average about three times as much time begging towards the larger female as they did towards the smaller one (Table 1; Figure 2a), confirming that larvae begged more towards the large female. We next tested between two potential behavioural mechanisms underpinning this preference; that is, whether larvae begged more when they were in close contact with the larger female or whether larvae spent more time in close contact with the larger female. We found that larvae spent more time in close contact with the larger female than expected due to chance (Wilcoxon signed-rank test: $V = 180$, $P = 0.04$; Figure 2b). However, there was no evidence that larvae begged more when they were in close contact with the larger female as opposed to when they were in close contact with the smaller

one (Table 1; Figure 2c). Thus, our results show that larvae begged more towards the larger female simply because they spent more time in close contact with her.

Discussion

Here we show that larvae in the burying beetle *N. vespilloides* begged more towards the larger female when given a simultaneous choice between two dead females: one larger and one smaller. We predicted that larvae would beg more towards the larger female given that larger females provision more food than smaller ones (Steiger 2013) and that begging incurs costs to larvae (Andrews and Smiseth 2013; Takata et al. 2019). Thus, our results support the hypothesis that offspring beg more towards the adult that is likely to provision them with more food, thereby maximising the offspring's returns on begging. There is support for this hypothesis from prior work on species with biparental care showing that offspring beg more towards parents of the sex that provisions the most food (Kölliker et al. 1998; Roulin and Bersier 2007; Dickens et al. 2008; Suzuki 2015; Paquet et al. 2018). Our study adds to this work by showing that offspring have preferences based on parental attributes other than sex, including body size.

We also show that larvae spent more time in close contact with the larger female than with the smaller one (Table 1; Figure 2a), whilst there was no evidence that larvae begged more when they were in close contact with the larger female (Table 1; Figure 2c). These results provide valuable insights into the behavioural mechanisms for why larvae beg more towards the larger female by showing larvae do so simply as a consequence of spending more time in close contact with her (Figure 2b). Larvae may spend more time in close contact with the larger female because larger females provision more food, as shown by a prior study on *N. vespilloides* (Steiger 2013). However, there are alternative explanations for why larvae spent more time in close contact with the larger female. First, if larvae move randomly within the

container, they may end up more often underneath the larger female simply by chance. This explanation seems unlikely given that there was no evidence that larvae moved randomly within the container. The larvae spent on average 92% of their time underneath one of the two females. Yet, the surface area covered by the two females (including the width of their pronotum around the females to match our criteria for determining whether larvae were in close contact with a given female), made up only 5.5% of the area of the container. We also note that the larvae were already underneath the two females by the time we started our observation session, only 5 min after we had placed the larvae in the container. Keeping in mind that we placed the larvae away from the two females at the start of the experiment, this suggests the larvae moved quickly in the direction of the two females. Second, larvae might approach females for protection and shelter, spending more time in close contact with the larger female if larger females are better at protecting larvae from potential threats. For example, in our study species, conspecific intruders pose a threat to the larvae as they may commit infanticide in order to attempt to takeover the carcass (Trumbo 2007; Trumbo and Valetta 2007, Georgiou Shippi et al. 2018). There is also evidence that larger females are stronger competitors against conspecifics than smaller females (Otronen 1988; Trumbo 2007). Thus, we cannot rule out the potential explanation that larvae may beg more towards the larger female as a consequence of being close to her for protection.

Our results imply that larvae somehow assessed the body size of the two females. As our study species normally breeds underground in complete darkness (Scott 1998), it is unlikely that larvae did so based on visual cues. Instead, larvae might assess differences between females based on behavioural, acoustic and vibrational cues that reflect body size. Although we cannot rule out that such cues play a role when larvae interact with live females, it seems unlikely that they could explain our results given that we used dead females as stimuli to trigger larval begging. Potentially, larvae may use tactile cues to assess female size

once they had approached the two females. There was some indication that larvae moved between the two females (on average, one larva moved between each scan), but there was no evidence that larvae moved in a specific direction; that is, from the smaller towards the larger female. Alternatively, larvae may assess differences in body size between females at a distance based on chemical cues, such as cuticular hydrocarbons (CHCs) and methyl geranate (Steiger et al. 2007; Smiseth et al. 2010; Steiger et al. 2011; Engel et al. 2016). Such chemical cues are present on dead parents, stimulate larval begging (Smiseth et al. 2010), and although CHCs are not volatile, they break down into volatile organic compounds when exposed to air and water vapour (Hatano et al. 2020). Thus, there is now a need for studies that compare CHC profiles of different-sized females.

We investigated whether offspring beg more towards larger adults in the context of communal breeding for practical reasons because it allowed us to exclude potential confounding effects due to other attributes of adults, such as their sex or breeding status. Nevertheless, we suggest that offspring preferences for larger adults may also be found in other contexts, such as biparental care, cooperative breeding and uniparental care (Table 1). In the context of biparental care, there is evidence that offspring beg more towards the parent of the sex that provisions the most food (Köllicker et al. 1998; Roulin and Bersier 2007; Dickens et al. 2008; Suzuki 2015; Paquet et al. 2018). Thus, demonstrating that offspring beg more towards the larger parent will require designs that can separate between offspring responses to parental body size and sex. Furthermore, in species where there are sex differences in body size, offspring preferences for larger adults may potentially explain why offspring beg towards parents of a particular sex. This is unlikely to be the case in our species because there are no sex differences in body size in *N. vespilloides* (Paquet et al. 2018). Similarly, offspring may beg more towards larger adults in the context of cooperative breeding, where offspring are provisioned food by parents that are assisted by non-breeding helpers (Vehrencamp 2000;

Koenig and Dickinson 2004). In this context, there is some evidence that offspring beg more towards their parents than towards the helpers (Fortuna 2016), and such preferences may be based on adults breeding status (breeders or helpers) or body size if there are differences in body size between parents and helpers. Finally, there may offspring preferences for larger adults in the context of uniparental care, although it is less obvious that this would be the case given that offspring would have no opportunity to choose between different adults.

Nevertheless, we suggest that offspring might have such preferences even in this context provided that offspring can choose between obtaining food by begging from their parent or finding food for themselves (Smiseth et al. 2003) and that begging incurs costs to offspring (Haskell 1994; Redondo and Castro 1992; Kilner 2001; Andrews and Smiseth 2013). Thus, offspring preferences for larger adults may occur in the context of uniparental care where offspring are only partially dependent on their parents, as in *N. vespilloides* (Smiseth et al. 2003), or where there is a transition period from complete dependence on parents for food towards full independence, as in many birds and mammals.

Our study has important implications for our understanding of parent-offspring communication. It is well established that offspring adjust their begging behaviour in response to changes in their own state, such as their hunger state (Kilner and Johnstone 1997; Smiseth and Moore 2004, 2007), their long-term need (Price et al. 1996) or their inbreeding status (Mattey et al. 2018). Here we show that offspring also adjust their begging behaviour in response to female body size, an attribute that predicts the ability of female parents to provision their offspring with food (e.g. Bosch and Vicens 2006; Tveera et al. 1998; Landete-Castillejos et al. 2003; Steiger 2013). Traditionally, parent-offspring communication is described as a process where begging offspring signal their needs, thereby playing the role as senders, and parents respond to the offspring's signals, thereby playing the role as receivers. Our study suggests that parent-offspring communication is more complex as begging

offspring also act as receivers by responding to cues from their parents. Thus, it seems more appropriate to describe parent-offspring communication as a two-way process where both parents and offspring act as senders and receivers, adjusting their behaviour based on signals or cues produced by each other.

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Table 1: Summary of our statistical approach and our results concerning whether larvae beg more towards larger females, and this was because larvae begged more towards larger females when in close contact with them, or because larvae spent more time in close contact with larger females.

| | Model | | Results | | |
|--|--|---|----------|----|------------------|
| | Generalised linear mixed model (GLMM) | | χ^2 | df | <i>P</i> |
| Overall time spent begging per larva in the brood | Fixed effect: Female status (Larger/Smaller) | Random effects: Brood ID, Observation level | 12.7 | 1 | <0.001 |
| Time spent begging per larva in the brood when in close contact the larger or smaller female | Fixed effect: Female status (Larger/Smaller) | Random effects: Brood ID, Observation level | 0.005 | 1 | 0.942 |

Note: Statistically significant *P* values (<0.05) are shown in boldface.

Figure legends

Figure 1. Experimental design used to test whether larvae spend more time begging towards a larger female over a smaller female. At the beginning of the behavioural observation, we placed the brood of 10 larvae equidistant from the two females (a). We then recorded the amount of time that larvae spent begging towards each female and the amount of time that larvae spent in close contact with each female (i.e. at a distance less than or equal to the female's pronotum length) (b).

Figure 2. Mean overall proportion of time spent begging per larva in the brood towards the larger and smaller female (a), and mean proportion of time spent begging per larva in when in close contact with either the larger female or the smaller female (b), and mean proportion of time spent in close contact with the larger female relative to time spent in close contact with the smaller female (c). The dash line in (c) represents the null expectation when larvae associated as much with the larger female as with the smaller one. Black dots and error bars represent mean \pm SE.